

OPERCULAR REGULATION IN THE POLYCHAETE *HYDROIDES*
DIANTHUS (VERRILL, 1873). I. OPERCULAR ONTOGENY,
DISTRIBUTION AND FLUX¹

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The cosmopolitan polychaete *Hydroides* is usually found subtidally at moderate depths, but may be seen occasionally on rocks along the shoreline. The animals spend their post-larval life in calcareous tubes attached to substrates such as rocks, mollusc shells, pilings and ship bottoms.

In this genus the head consists of a prostomium bearing two hemicirclets of ciliated and pinnuled branchiae as the only appendages. Normally these are the sole exposed portions of the body and they serve as respiratory, feeding and sensory organs. Two dissimilar opercula attached to the dorsal base of these structures are modified branchiae. The larger operculum functions as a tube plug. In its mature form it is modified for defensive purposes by having a non-pinnuled, thickened stalk and an enlarged tip consisting of two cup-shaped structures, one arising from within the other (Fig. 1a). On the side opposite the functional operculum is a small, rudimentary operculum with a swollen but otherwise undifferentiated tip. The functional operculum may be associated with either the left or the right branchial half-circle, hence the designation of animals as "left-handed" or "right-handed."

Zeleny (1905, 1911), in his classical account of the ontogeny of *Hydroides dianthus* larvae, established that the initial operculum developed from the middle member of the original three branchiae on the left. These branchiae were provided with a number of elongated and ciliated respiratory pinnules. The pinnules on the opercular branchia soon dropped off or were resorbed, leaving a simple primary functional operculum on the now naked stalk. Shortly thereafter the middle of the three branchiae on the right dropped off and a primary rudimentary operculum, consisting of a short, undifferentiated stalk, developed at the site of autotomy. Two unchanged branchiae then remained on each side. One or two new branchiae were added ventrally, but no other changes occurred until the animal was about six months of age, when the primary functional operculum on the left was autotomized. The primary rudimentary operculum on the right simultaneously enlarged to become a secondary functional operculum which had a mature, two-tiered structure. The residual stump on the left formed a secondary, mature type of rudimentary operculum. Therefore all animals should be right handed at this stage. No further observations were made by Zeleny.

¹ This work constitutes a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy from the Division of Biological and Medical Sciences, Brown University, Providence, Rhode Island.

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While working at Woods Hole, it became apparent that the development of many *Hydroides dianthus* larvae could not be reconciled with this account. Observations suggested that only the initial appearance of the functional operculum is programmed and that thereafter the animals follow a variety of pathways.

That the position of the adult functional operculum can be reversed was first shown by Zeleny (1902, 1905). After amputation of the functional operculum the rudimentary operculum differentiated into a functional one, while the stump of the former functional operculum regenerated a rudimentary structure. Zeleny proposed that natural physiological reversals might occur, although he had no direct evidence to support this suggestion. Ichikawa and Takagaki (1942) found that, during several months of maintenance, four of 17 asymmetric juveniles of *Hydroides ezoensis* reversed. They postulated that this was due to physiological aging of the functional operculum, which would eventually be discarded.

The existence of occasional individuals with two functional opercula has not been satisfactorily explained. Rioja (1919) regarded them as throw-backs to an ancestral bi-operculate type. La Greca (1949, 1950), finding that double-operculate animals in his laboratory population of *H. norvegica* were regenerating branchiae, proposed that involution of, or injury to the branchiae could allow the rudimentary operculum to develop. During starvation or other suboptimal conditions, natural involution of branchiae can occur but double functional opercula rarely form during subsequent regeneration (Greuet, 1962). Bi-operculate animals can be experimentally produced by the simultaneous removal of both opercula (Zeleny, 1905; Okada, 1933; Abeloos, 1952a), by a transverse thoracic section (Zeleny, 1902, 1905; Okada, 1933; Abeloos, 1952a; Cresp, 1964), or by the excision of at least one-half of the branchiae (La Greca, 1950). It is dubious whether any of these conditions would arise frequently enough to account for the presence of substantial numbers of these animals in a natural population.

This study investigates opercular development, opercular dynamism, and population structure in specimens of *Hydroides dianthus* at Woods Hole.

METHODS

Specimens of *Hydroides dianthus* of various ages were dredged from a depth of 60 feet in Buzzard's Bay by the Supply Department of the Marine Biology Laboratory, Woods Hole, Massachusetts. During the breeding months (June through September) tiny juvenile worms may be found interspersed among the adult tubes on mollusc shells and rocks. These immature animals with their tubes were carefully removed from the substrate with fine forceps. Only individuals less than 3 mm in body length were utilized. In some cases the fragile tube shattered during the process, but generally enough remained to enable the animal to repair and extend it (*cf.* Neff, 1969). The animals were placed in small vials filled with 20 ml of sea water, which was changed every few days and kept at ambient temperatures (20–23° C). As the animals did not attach to the bottoms of the vials, they could be easily removed with a Pasteur pipett. For experimental manipulations, specimens were placed in a drop of sea water on a glass slide, and opercular and branchial amputations were performed with a No. 5 forceps and a micro-dissecting needle.

After complete or partial removal from their tubes, adult animals were maintained in fingers bowls covered with cheesecloth. The bowls were submerged in a

sea water table, and were cleaned frequently to remove algal deposits. The most expeditious method of removing adults from their tubes was by cracking and removing the posterior end of the tube. The worm was then pushed out through this opening with a piece of fine polyethylene tubing.

For field population studies wooden frame boxes were enclosed with nylon screening. An opening was made in one side of the screening to permit small predators to enter. Intact specimens on shells were placed inside the boxes and were submerged in Vineyard Sound in approximately 20 feet of water. The bottom in the chosen location was silty, rather than rocky, as is the usual habitat of these animals. The remaining animals in these studies were maintained in sea water tables in the laboratory, as described above. Observations on both groups of animals were made at one-week intervals.

Experimental groups were compared using the chi-square distribution. Chi-square 2×2 contingency tables were used in these calculations and manipulations were performed on a Hewlett Packard 9100A calculator.

OBSERVATIONS

Ontogeny of the branchiae and opercula

The early development of *Hydroides* embryos is typical of other annelids, and the trochophore is indistinguishable from that of other Serpulid genera. The cleavage and larval stages of Serpulids have been described in detail by Conn (1884), Soulier (1898), Shearer (1911), Segrove (1941) and Sentz-Braconnet (1964). At metamorphosis the larvae settle on the substratum and begin to secrete calcareous tubes. According to Zeleny (1905) and Wisely (1958), just prior to this time the protuberant head of the free-swimming larva differentiates into a more flattened structure with dorso-lateral lobes. Three or four branchial rudiments appear simultaneously from each of these lobes (Fig. 1b). These stumpy, ciliated rudiments elongate and develop minute protuberances which indicate the future position of respiratory pinnules. These grow rapidly as the branchial filaments enlarge. At the stage when the primary operculum first appears (about four weeks after fertilization) the worm possesses three symmetrical, pinnuled sets of branchiae (for details of branchial development, see Zeleny, 1905, 1911).

The first indication of an operculum is a swelling at the apex of the left median branchia (Branchia II). The orientation of this operculum appears to be invariable in the larvae of most species of *Hydroides* examined but Ichikawa and Takagaki (1942) found that in 5 of 77 *H. exoensis* juveniles the initial operculum appeared on the right side. The terminal swelling of the branchial filament enlarges into a small, funnel-shaped opercular cup perched on top of an otherwise unexceptional pinnuled branchia. This structure will be henceforth referred to as the branchial operculum (Fig. 1c). The opercular branchia has two long pinnules in *H. dianthus*, although eight were reported by Zeleny in the same species (1905).

The initial sample consisted of 55 pre-opercular juveniles. The number of animals in the groups below is small because of death or lack of opercular development by many larvae under laboratory conditions.

In three animals the branchial operculum originated as described above and within three to 14 days the pinnules on the opercular branchia were lost. The

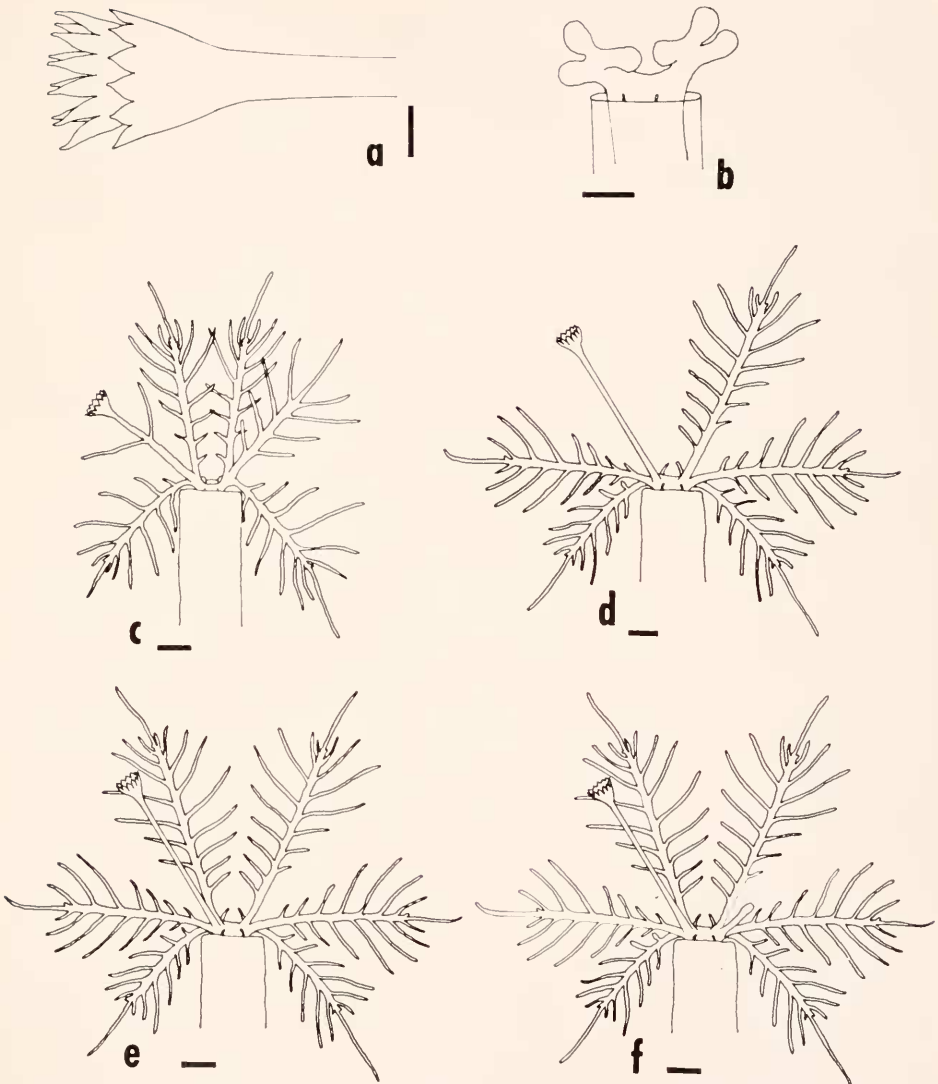


FIGURE 1 (a) A mature functional operculum of *Hydroides dianthus*, with a characteristic double-cupped structure and thickened spines, marker length = 1 mm; (b) head of a post-metamorphic *H. dianthus* juvenile, demonstrating the branchial rudiments. The animal at this time is approximately 1 mm in length, marker length = 0.1 mm; (c) dorsal view of a 1 mm juvenile with a branchial operculum on the left median branchia. The most anterior branchiae may or may not be pinnuled at this time. The animal is shown projecting from its tube, marker length = 0.1 mm; (d) dorsal view of a juvenile with a left primary functional operculum and asymmetric distribution of branchiae, marker length = 0.1 mm; (e) dorsal view of a juvenile with a left primary functional operculum and symmetric branchiae (modified from Zeleny, 1905), marker length = 0.1 mm; (f) a juvenile with a left primary-type functional operculum and a primary rudimentary operculum on the right (modified from Zeleny, 1905), marker length = 0.1 mm.

corresponding right branchia was not autotomized at any time to make space for a primary rudimentary operculum, as Zeleny (1905, 1911) and Wisely (1958) noted. Therefore these animals had three pinnate branchiae on the right side and two on the left side, in addition to the non-pinnuled operculum, which may now be called the primary functional operculum (Fig. 1d). The majority of the juveniles which survived through the developmental period, however, did not exhibit this branchial asymmetry. Each of these retained three pairs of pinnuled branchiae throughout early development. In six individuals the opercular cup disappeared from the tip of the left Branchia II, and a non-pinnuled primary functional operculum appeared on the left, in addition to the three intact branchial pairs (Fig. 1e). These animals had three sets of pinnuled branchiae but were rendered asymmetric by the presence of the primary functional operculum on the left side. In four other larvae, the operculum formed was a primary rudimentary type, which ceased to develop further. Three remaining larvae lost the branchial operculum without any ensuing opercular formation.

The numerical imbalance between individuals showing branchial symmetry and asymmetry was sustained in older animals. Six of seven with a left primary-type functional operculum but no rudimentary one had symmetrical branchiae. This is more difficult to explain than the cases in which the primary operculum is derived from the second branchia by a simple loss of pinnules from the branchial stalk (Zeleny 1905, 1911). One possible explanation for this phenomenon assumes the formation of a new branchia on the left to replace the one which has lost its pinnules and become an operculum. However, regenerating branchiae are never observed under these circumstances. A more plausible alternative is that the left median branchia does not lose its pinnules, but that the opercular cup at the apex of this branchia is autotomized and the primary functional operculum formed *de novo* from the branchial base. In such an eventuality there will be a developmental difference between the transient branchial operculum which appears on the branchial apex and the primary functional operculum which arises independently on the same side. It should be emphasized that, although the branchial filaments and the opercular stalk are almost identical in morphology and in histological structure, none of the opercula subsequent to the branchial one is derived directly from the branchiae; rather they develop from the basal portion of the branchial crown. The tissue of the branchial base has the capability of producing new opercular structures at all stages of development.

The probability of a non-branchial origin of the primary functional operculum is supported by the following observation. Over a period of five weeks the branchial filament supporting the opercular cup in one animal became progressively more attenuated at the terminal end until at last the cup was autotomized, leaving a normal-appearing branchia. Consequently this worm had three pairs of branchiae but no operculum. Subsequently a rudimentary type of operculum appeared on the left side, and the animal did not change thereafter. While this phenomenon was observed only once, loss of the branchial operculum normally occurs soon after its formation, and the chances of detecting its loss would be slight. This particular animal was unusual in having retained the branchial operculum for almost five weeks. In addition, several larvae were found with symmetrical branchiae and an operculum developing on the left side. This also suggests a *de novo* formation of the primary operculum.

However the primary functional operculum originates, it is dropped within a few weeks and a rudimentary operculum may develop on the right side. Eight specimens, after losing the primary functional operculum, replaced it with a primary rudimentary one which subsequently developed into another primary-type functional operculum. In three of these animals there was a contemporaneous rudimentary operculum (Fig. 1f); nevertheless, the primary functional operculum was preferentially replaced by another functional one on the same (left) side and no opercular reversal occurred at this time. In three additional animals, however, the loss of the primary functional operculum signaled the primary rudimentary operculum present on the right to differentiate into a functional operculum. These proved to be very transient and were rapidly replaced by rudimentary structures again. In other animals the primary rudimentary operculum which developed on the left after the loss of the primary functional one did not differentiate into a functional one, and another rudimentary operculum was usually formed on the right. In most cases (22 out of 33) these animals retained the two rudimentary opercula for a lengthy period of time. They may represent a quiescent stage, such as the six-month hiatus reported by Zeleny (1905) between the appearance of the primary opercula and the first reversal. In a few individuals, one or the other of the rudimentary opercula would appear enlarged or swollen, only to revert to normal size. It was as though the presence of a second rudimentary operculum inhibited the first from developing into a functional type.

In addition to the juveniles collected at a pre-opercular or primary opercular stage, there were 65 specimens with a functional operculum already present on the right side and a rudimentary one on the left. These animals were more mature than a large majority of the left-handed specimens, as indicated by their size, the opacity of the body and tube, the mature form of their opercula and the appearance of pigmented stripes on the functional operculum. Eleven of these animals autotomized the functional operculum and regenerated a rudimentary operculum in its place without reversal. The remainder died or did not change during the observation period.

Population composition

In order to determine whether opercular changes occur naturally in *Hydroides dianthus*, it was necessary to ascertain the normal population composition. Few quantitative studies of Serpulid populations exist and, except for the genus *Hydroides*, conclusions about opercular distribution have been made on the basis of small numbers of animals. Zeleny (1902, 1905) found a slight predominance of right-handed specimens in *H. dianthus*, *H. uncinata*, and *H. pectinata* collections. Ichikawa and Takagaki's (1942) survey of an enormous *H. czocensis* population from Japan gave similar results. No statistical tests were used by these investigators, but they all assumed a preponderance of right-handed animals. Application of chi-square tests to their data indicated that none of these populations differed significantly in "handedness" from a 50-50 distribution, thereby corroborating the observations of Ludwig and Ludwig (1954) who worked with the European species, *H. norvegica*.

Since opercular distribution in a population might vary with age and sexual maturity, the worms used in this study were separated into the following categories: Adult—large animals with heavily-calcified tubes and approximately 30 pigmented

branchiae; Young—smaller animals with thin delicate tubes and fewer, lightly-pigmented branchiae; and Juvenile—very young post-metamorphic animals, 3 mm or less in total length, with extremely thin translucent tubes.

According to Grave (1933) and Hill (1967), under optimal conditions individuals of the genus *Hydroides* become sexually mature six to eight weeks after metamorphosis. Therefore the first two samples should both be of reproductive age.

One thousand, one hundred and twelve adult, 952 young and 209 juvenile specimens of *Hydroides dianthus* were tabulated. Table I presents the distribution of left- and right-handed individuals in this population. Neither adult nor young animals differed from a 50-50 distribution of left- and right-handed animals. In contrast, the juveniles taken as a group were heavily skewed in favor of left-handed specimens and, consequently, the proportions of the juvenile population differed significantly from that of both adult ($P < 0.005$) and young ($P < 0.005$) populations. Ichikawa and Takagaki (1942), Ludwig and Ludwig (1954) and H. W. Ludwig (1957) also reported that juvenile specimens were predominantly left-handed.

The juvenile group was subdivided according to size into three categories. Group A was 1.5 mm or less in length; Group B, 1.5 to 2 mm; and Group C, 2 to 3 mm. Of these only Group A, the youngest animals, did not demonstrate an equal

TABLE I

Distribution of left-handed, right-handed and bi-operculate animals in a population of Hydroides dianthus. Abbreviations are: LH, left-handed specimens; RH, right-handed specimens; B, bi-operculate specimens

	N	%	Chi-square value (Variation from 50-50 distribution excluding bi-operculate animals)	P
Adult	LH 531	(43.8)	0.00	$P > 0.975$
	RH 528	(43.6)		
	B 153	(12.6)		
Young	LH 389	(40.9)	0.23	$0.9 > P > 0.5$
	RH 408	(42.8)		
	B 155	(16.3)		
Juvenile groups A (<1.5 mm)	LH 56	(8.84)	20.94	$P < 0.005$
	RH 8	(12.1)		
	B 2	(3.0)		
B (1.5-2.0 mm)	LH 36	(45.6)	0.19	$0.9 > P > 0.5$
	RH 31	(39.2)		
	B 12	(15.2)		
C (2-3 mm)	LH 23	(35.9)	0.09	$0.9 > P > 0.5$
	RH 26	(40.4)		
	B 15	(23.4)		
Combined	LH 115	(55.0)	7.60	$0.01 > P > 0.005$
	RH 65	(31.1)		
	B 29	(13.9)		

distribution of left- and right-handed individuals (Table I). It therefore appeared that the difference between the older worms and juvenile worms was attributable entirely to Group A, as neither Group B nor Group C was statistically different from the adult ($0.9 > P > 0.5$) or young ($0.5 > P > 0.1$) samples.

The proportion of animals with two functional opercula in the three populations was more variable than the left-right ratios, ranging from 3 to 23% of the population in question (Table I). Comparisons of these values indicate that, whereas adult and young populations did not differ in left-right ratios, the young group had a significantly higher proportion of bi-operculate specimens ($0.25 > P > 0.01$). Neither older sample varied from the juvenile group as a whole in this regard. However, the proportion of bi-operculate animals in the adult population was significantly higher than that of Group A and lower than that of C (in both cases, $0.025 > P > 0.01$). The young animals had significantly more bi-operculate forms than A ($P < 0.005$), but were not different from B and C. Groups B and C did not differ from each other. Thus the older portions of the juvenile population resembled the young rather than the adult group in the distribution of bi-operculate individuals. The animals of juvenile group A had only reached the earlier stages of opercular development and many still had only the primary functional operculum, whereas the adults showed a marked decline in bi-operculate specimens from the proportions in the younger age groups.

In the course of examining approximately 5000 specimens of *Hydroides dianthus*, I encountered two animals with supernumerary opercula. Each had two rudimentary and one functional operculum. In one, both rudimentary opercula branched from the same peduncle; in the other, the functional operculum and one of the rudimentary ones were joined at the base. These individuals were apparently the result of developmental aberrations although the opercula themselves were morphologically normal. Zeleny (1905) and La Greca (1950) also reported finding an animal with three opercula.

Opercular Flux

The ability of these serpulids to replace a missing functional operculum by the development of the rudimentary one enhances the probability that reversal might be a natural event. Collected specimens were occasionally found with a developing functional operculum on one side and a new rudimentary operculum regenerating from the opercular stump on the opposite side. Whether this reversal was provoked by accident or by an intrinsic physiological process has not been determined.

To study possible natural variations in *Hydroides* populations, a simple format was used in which left-handed, right-handed and bi-operculate animals were maintained separately for observation. The following groups were observed at intervals of one week for a six-week period: *Group 1*: Adult, left- and right-handed animals kept in the laboratory; *Group 2*: Adult, bi-operculate animals kept in the laboratory; *Group 3*: Adult animals of all types, kept in the field; *Group 4*: Young left- and right-handed animals kept in the laboratory; *Group 5*: Young bi-operculate animals kept in the laboratory. Because of the excellent survival rate of the young animals, it was possible to follow them for 6–8 weeks. Animals of Groups 4 and 5 which had undergone some change were segregated into the following four

categories. All were maintained in the laboratory. *Group 6*: Young left- and right-handed animals from Group 4, which had reversed during the course of observation; *Group 7*: Young left- and right-handed animals from Groups 4 and 5 which had previously been bi-operculate; *Group 8*: Young animals which had lost their functional opercula, from all groups of young animals; *Group 9*: Young animals from Groups 4 and 7 which became bi-operculate during the course of the experiment, but which were not so at the beginning.

Group 1: ($N = 77$) *adult left- and right-handed animals*. The majority of these animals did not change during any one week. Those which did had either autotomized the functional operculum, in which case the rudimentary operculum had enlarged (reversal) or, alternatively, the rudimentary operculum had developed although the functional one remained intact. The latter process resulted in a bi-operculate animal. In a few of these cases, the functional operculum was obviously degenerating.

A constant rate of change was observed from one week to the next in this group except for the last two of the six weeks. By this time the animals may have been in a precarious physiological state. Data are given in Table II, Column 1.

Group 2: ($N = 71$) *bi-operculate adult animals*. The only alteration observed in bi-operculate animals was the autotomy of one of the opercula and its subsequent replacement by a rudimentary operculum. Thirty-seven of the original 71 animals underwent this change, 21 died without change, and only seven remained bi-operculate after three weeks. This is an average change of 37.7% per week. Note that this rate of alteration is much greater than changes in asymmetric animals (Group 1), and thus bi-operculate worms would be rapidly converted to left- and right-handed individuals under these circumstances.

In most bi-operculate individuals one operculum is more mature than the other, and animals can be categorized on this basis. Those in which the left operculum was older were denoted as L/B ($N = 40$); those in which the right one was older, R/B ($N = 31$). In general the animals lost the more mature operculum. Seventeen of the L/B individuals became right-handed, and only two autotomized the younger right operculum to become left-handed. Of the R/B individuals, 16 lost the right operculum, and two lost the less-developed left operculum. The remainder in both groups died. Therefore almost 90% of the surviving animals autotomized the older operculum, a process which results in reversal of the prior asymmetry.

Group 3: ($N = 127$) *adult animals maintained in Vincyard Sound*. As it proved impossible to distinguish left-handed and right-handed animals in their tubes with an accuracy of more than 70 to 80%, they were classified as to whether they had mature, immature, double or aberrant functional opercula.

This group was initially composed of 112 asymmetric individuals, 10 bi-operculate ones, two without one of the branchial half-circllets, one without any visible opercula, and one which had lost both head and upper thorax. Observations were unfortunately curtailed the third week of observation by heavy silting of the habitat and consequent mortality.

The changes occurring in originally normal, asymmetric animals consisted of (a) loss of the mature functional operculum and its replacement by a young, developing one; (b) loss of the mature functional operculum without any observable replacement; (c) doubling, *i.e.* formation of bi-operculate individuals from left- or right-handed animals, (d) loss of the opercular cup, and (e) loss of branchiae

TABLE II
*Comparison of changes in left-handed and right-handed individuals
of groups 1, 3, 4, 6, and 7*

Initial sample size	Group 1 Laboratory maintained adults N = 77	Group 3 Field adults N = 112	Group 4 Young animals N = 349	Group 6 Young LH&RH animals changed N = 50	Group 7 Young LH&RH animals formerly bi-operculate N = 30
First week	N = 67	N = 105	N = 160	N = 46	N = 22
Reversal	1 (1.5%)	10 (9.5%)	23 (14.4%)	6 (13.0%)	2 (9.1%)
Bi-operculate	2 (3.0%)	1 (1.0%)	10 (6.3%)	—	3 (13.6%)
No visible operculum	—	19 (18.1%)	4 (2.5%)	5 (10.9%)	—
Other change	—	2 (1.9%)	—	—	—
Total change	3 (4.5%)	32 (30.5%)	37 (23.1%)	11 (23.9%)	5 (23.7%)
Second week	N = 47	N = 61	N = 129	N = 26	N = 15
Reversal	2 (4.3%)	4 (6.6%)	16 (12.4%)	1 (3.8%)	2 (13.3%)
Bi-operculate	1 (2.1%)	1 (1.6%)	2 (1.6%)	—	—
No visible operculum	—	11 (18.0%)	2 (1.6%)	—	1 (6.7%)
Other change	—	6 (9.8%)	3 (2.3%)	—	—
Total change	3 (6.4%)	22 (36.1%)	23 (17.8%)	1 (3.8%)	3 (20.0%)
Third week	N = 30	N = 0	N = 95	N = 21	N = 10
Reversal	1 (3.3%)	—	6 (6.3%)	2 (9.5%)	—
Bi-operculate	1 (3.3%)	—	3 (3.2%)	—	—
No visible operculum	—	—	7 (7.4%)	—	—
Other change	—	—	—	—	—
Total change	2 (6.7%)	—	16 (16.8%)	2 (9.5%)	—
Fourth week	N = 18	N = 0	N = 74	N = 16	N = 8
Reversal	—	—	7 (9.5%)	3 (18.8%)	—
Bi-operculate	1 (5.6%)	—	2 (2.7%)	1 (6.2%)	1 (12.5%)
No visible operculum	—	—	2 (2.7%)	—	—
Other change	—	—	3 (4.1%)	—	—
Total change	1 (5.6%)	—	14 (18.9%)	4 (25.0%)	1 (12.5%)
Fifth week	N = 7	N = 0	N = 59	N = 11	N = 4
Reversal	—	—	7 (11.9%)	3 (27.3%)	—
Bi-operculate	—	—	1 (1.7%)	1 (9.1%)	—
No visible operculum	—	—	2 (3.4%)	—	—
Other change	—	—	—	—	—
Total change	—	—	10 (16.9%)	4 (36.4%)	—
Sixth week	N = 2	N = 0	N = 44	N = 0	N = 1
Reversal	—	—	2 (4.5%)	—	—
Bi-operculate	—	—	—	—	—
No visible operculum	—	—	—	—	—
Other change	—	—	—	—	—
Total change	—	—	2 (4.5%)	—	—
Sum	N = 171	N = 166	N = 561	N = 120	N = 60
Reversal	4 (2.3%)	14 (8.4%)	61 (10.9%)	15 (12.5%)	4 (6.7%)
Bioperculate	5 (3.0%)	2 (1.2%)	18 (3.2%)	2 (1.7%)	4 (6.7%)
No visible operculum	0	30 (18.1%)	17 (3.0%)	5 (4.2%)	1 (1.7%)
Other change	0	8 (4.8%)	6 (1.1%)	0	0
Total change	9 (5.3%)	54 (32.5%)	102 (18.2%)	22 (18.3%)	9 (15%)

and/or some thoracic segments. Data from this sample are found in Table II, Column 2.

Originally bi-operculate animals did not remain bi-operculate, and either one or both of the functional opercula was rapidly autotomized. Loss of both opercula was not observed in bi-operculate specimens of Group 2, above.

Other animals with missing parts usually regenerated these structures. Severe injury resulted in the subsequent disappearance of the animal.

Opercular modifications in this population were considerably augmented in comparison with the adult group maintained in the laboratory. During each of the week-long periods, more than one-third of the animals varied from their previous state. At the end of the first week, 36.4% of the worms had altered; by the second, a further 39.8% of the unchanged animals had done so. Only 34.8% of the 112 original right- and left-handed animals remained unchanged for the two periods, and only one of the bi-operculate individuals sustained both opercula for more than one week.

Animals with a young functional operculum and at least some of those with no visible operculum were apparently in the process of reversing. If one assumes that all of these animals were doing so, then by the end of the first period, almost 30% (29 of 105) of the surviving normal worms were reversing, and almost 25% (15 of 61) of the asymmetric animals surviving to the second week did likewise. A comparable figure for the laboratory-maintained adults (Group 1) would be approximately 4%.

The incidence of animals with missing branchiae, segments, opercula, or parts thereof presumably reflects the activity of predators. The incidence of predation cannot be exactly determined because the animals which disappeared from their tubes during the course of the experiment may have succumbed to other environmental factors.

Group 4: (N = 349) young left- and right-handed animals. Many of these animals died during the early portion of the experiment, but subsequently survival rates were excellent. Each animal was observed for six weeks, or until the termination of the experiment.

The changes observed in these young animals were similar to those found in the comparable older specimens (Group 1); *i.e.*, opercular reversal, doubling, and occasional aberrations such as opercular or branchial loss. Total variation was considerably greater than that in Group 1, but much lower than that of the adults kept in the field (Group 3). The data from the group appear in Table II, Column 3.

Group 5: (N = 50) young bi-operculate animals. After one week, 11 of the 12 worms observed had autotomized one of the opercula. Four of these had become left-handed and seven, right-handed. The remaining animal had lost head and thorax and was discarded. One sample of 11 animals was not observed until two weeks after the beginning of the experiment, and of these, five had become left-handed and six, right-handed.

Young bi-operculate specimens appeared to be highly labile, maintaining this state for a short time only. All of the individuals then reverted to an asymmetric opercular pattern, and they did so much more rapidly than the older animals (Group 2). Adult bi-operculate animals in the field (Group 3) however, demonstrated as rapid a turnover as these younger animals.

The tendency of altered animals to repeat these changes was tested by segregating healthy specimens of Groups 4 and 5 into Groups 6 through 9.

Group 6: (N = 50) young asymmetric animals which had reversed. While seven animals did not undergo any subsequent changes for five consecutive weeks, a few others changed several times. The average rate of change proved to be almost the same as that of the original asymmetric population (Group 4). See Table II, Column 4.

As these animals were not all kept for a full six periods because of the termination date of the experiment in the autumn, the rate of variation given here may be somewhat low.

Group 7: (N = 30) previously bi-operculate young animals, now asymmetric. The rate of variation in such animals (*i.e.*, becoming bi-operculate or reversing) was similar to the corresponding rates of young asymmetric individuals (Group 4) or those which had previously reversed (Group 6). See Table II, Column 5.

Group 8: (N = 8) young animals without functional opercula. Four specimens had previously been right-handed, and four, left-handed, but one had been bi-operculate. They eventually regenerated new functional opercula, but half of them did not reverse, and regenerated a new functional operculum on the same side as the old one. No subsequent opercular changes were noted.

Group 9: (N = 17) young animals which became bi-operculate. Only two of the 14 survivors in this group were still bi-operculate after one week. One of these retained both functional opercula for two, and the other for three weeks before reverting to an asymmetric state. The rapid turnover is quite comparable to that in the animals of Group 5. In every case, the worm retained the younger operculum, resulting in a reversal of the initial asymmetry.

The animals of Group 9 were kept from one to five weeks longer, and during that time none of them demonstrated any further changes. The prior history of these animals is interesting, however. Six of the 17 had been bi-operculate at an earlier time during the experiment; five within the two previous weeks and one, within the five previous weeks.

Comparisons between groups

Groups 1, 3, 4, 6 and 7 (asymmetric animals) were compared with respect to two criteria: the incidence of reversals and the incidence of bi-operculate animals. Chi-square tests between the paired groups indicated that most groups had similar rates of reversal, with the exception of the laboratory-maintained adults, Group 1. The animals in this sample had a significantly lower proportion of individuals undergoing reversal than any of the other groups except Group 7; (for Group 3, $0.025 > P > 0.01$; for Groups 4 and 5, $P < 0.005$). Group 7 did not differ significantly from any of the other groups.

Most groups were approximately equivalent in the rate of production of bi-operculate animals. Less than 7% of the specimens became bi-operculate during any period in any group, and ordinarily the percentage was much lower. The highest production of bi-operculate specimens was found in Group 7, in which the incidence was significantly higher than among field adults of Group 3 ($0.025 > P > 0.01$), but not higher than any of the other groups.

The laboratory-maintained adults, then, did not reverse the positions of the opercula as frequently as did the young animals. Adults in the field, under more

stressful conditions than prevail in the laboratory, tended to lose opercula with high frequency, which suggests that many reversals in nature may occur as a result of trauma, rather than unprovoked autotomy. Young animals had an elevated frequency of opercular loss even in the laboratory, and therefore in the field they might have had a rate comparable to or exceeding that of the field-maintained adults of Group 3.

Opercular flux in juveniles

The deviation of both left- and right-handed juveniles with rudimentary opercula from the normal adult reversal pattern (see above) could be attributed to several things: nutrient deprivation (although there were algal growths and small plankton in the vials), a natural quiescent stage, or an undeveloped reversal mechanism in these young animals. Some insight into this problem is given by the observations described below.

A number of juveniles collected had two functional opercula, and in older samples as many as one-third were bi-operculate, the proportion increasing with augmented size and age of the animals. These bi-operculate juveniles are interesting with regard to the origin of the first mature type of functional operculum, which can be distinguished from a primary functional operculum by the presence of a secondary cup arising from the center of the proximal one. According to Zeleny (1905, 1911) each individual produced only one primary functional operculum. The animals then proceeded, upon the loss of this operculum, to develop a mature functional operculum by growth and differentiation of the rudimentary operculum which lies on the right side. In the present sample, no such regularity was observed in the time of appearance of this mature operculum, as most animals recapitulated the primary-type functional operculum more than once. This apparent randomness was emphasized by the behavior of the bi-operculate animals.

Fourteen bi-operculate juveniles were considered. Six of these had one mature and one primary-type functional operculum; the latter were present on either side. In five other individuals both opercula were of the mature type, and the remaining three had two primary-type functional opercula.

Of the four surviving animals of the first sample, three autotomized the primary-type operculum. Two of these had this operculum on the right; one, on the left. The preferential loss of the primary-type operculum supports the idea that at a particular point in ontogeny the primary operculum is succeeded by a mature operculum. The fact that the primary operculum may be located on either side indicates that prior reversals have occurred in at least some animals. The fourth animal in this group autotomized the mature-type operculum, and was left with the primary one. This suggests that there may be a transitional period during which the mature opercular form is not yet definitively established, and during which it may be supplanted by an immature structure. The animals in the second group were puzzling, as two of the three survivors autotomized the younger, developing mature operculum. Later the older operculum was also lost, to be replaced by a rudimentary operculum. The two surviving animals of the last sample both lost the left primary operculum. It seems that the bi-operculate state is a transient one, but the result is not immediate reversal of the prior opercular positions as in adult animals.

Experiments on pre-opercular animals

The period of experimental observation was two months, or until the death of the specimen. The animals in this group were all at stages prior to the appearance of the opercular cup. Either three or four pairs of branchiae were present. Only long-term survivors are enumerated. In the first group of 10 animals, the entire left or right branchial circle was extirpated. The branchiae removed were rapidly regenerated and a highly accelerated growth rate soon re-established the parity between the branchiae of the two sides. After one to two weeks the branchiae on the amputated side could not be distinguished in size or development from those on the opposite side. In eight of the ten survivors, no further development occurred within the observation period, but the remaining two developed a single rudimentary operculum. In one animal it appeared on the left; in the other, on the right.

The control animals were left to develop undisturbed. Of the four survivors, two formed an opercular cup within one week; the other two showed no opercular development. The difference between the control animals and the experimental animals indicates that removal of the branchiae retards opercular development even though normal branchial morphology is restored. The formation of primary rudimentary, rather than branchial opercula in two of the experimental animals suggests that these animals associated surgical removal of branchiae with loss of the operculum, and so the normal developmental pattern was disrupted by the trauma. In these cases the branchial opercular stage was by-passed.

Experiments on animals with branchial opercula

Basal excision of the left Branchia II with its associated branchial operculum yielded contradictory results. The development of one animal was so disturbed that only branchial regeneration occurred. A second worm produced two primary-type rudimentary opercula, and a third developed a primary functional operculum. This last response was also typical of two specimens in which the entire left branchial circle was removed together with the opercular branchia. The operculum was thereafter lost and replaced by a rudimentary one. A mature operculum developed on the right side in one specimen and the last surviving animal in this group regenerated the entire pinnuled branchial operculum.

Zeleny (1911), in somewhat analogous experiments, removed the upper stalk of the opercular branchia, or the opercular cup alone, but did not amputate the entire stalk. Either level of amputation resulted in the regeneration of the opercular cup from the severed end of the branchial filament. A peculiar feature in two of the animals was the appearance of a fleeting pre-opercular swelling on the tip of the right Branchia II, a feature which I found also in two undisturbed pre-opercular animals, but not in any of the experimental animals. In all cases the swelling was soon resorbed. Only one of the animals in the present experiment responded to total extirpation of the opercular branchia by regeneration of the original pinnuled form, in contrast to the results when only the upper half of the stalk is severed (Zeleny, 1911).

The four surviving control animals which were untreated retained their primary functional opercula for several weeks before replacing them with rudimentary ones, so that their development corresponded closely to that of the experimental animals.

Experiments on animals with primary functional opercula on the left

These animals had a primary functional operculum without pinnules on the left and no rudimentary operculum. The right branchial cirlet was severed at the base. The three surviving animals reproduced the missing branchiae and could not thereafter be distinguished from the control group.

In a second group of juveniles, the primary functional operculum was removed, with or without concomitant amputation of the left branchial apparatus. The primary functional operculum was replaced by a rudimentary one in four cases, and another primary-type rudimentary operculum formed later on the right side in two of them. The remaining two formed no opercula at all. At the termination of the experiment none of the rudimentary opercula had differentiated into functional ones. Two of the six surviving control animals retained the primary operculum throughout the observation; the other four replaced it with a rudimentary one.

Experiments on animals with both primary functional and rudimentary opercula

Sixteen juveniles had a rudimentary operculum in addition to a primary functional operculum, but the removal of the latter did not induce differentiation in the rudimentary one except in two individuals. In these two the rudimentary operculum enlarged into a mature type of functional operculum, and the animals became right-handed. One other individual formed a second primary-type functional operculum in place of the amputated one, but the remainder of the animals regenerated only rudimentary opercula (10) or no opercula at all (3) on the site of amputation.

Of the five surviving control animals, one retained the primary functional operculum during the entire experimental period. The others autotomized it and developed a rudimentary operculum in its place.

Experiments on animals with functional opercula on the right side

These were among the larger specimens, and they invariably had rudimentary opercula on the left side. Both opercula were of the mature type. When the functional operculum was cut off at the base, in eight of the ten specimens the rudimentary operculum enlarged into a functional one and the amputated side regenerated a rudimentary operculum. In the other two animals there was only replacement of the functional operculum by a rudimentary one. When the entire branchial crown, including the opercula, was removed, the entire apparatus regenerated. In two animals the functional operculum appeared on the left side; the other two produced rudimentary opercula on both sides. Opercular growth was retarded in these animals. Six of the eight surviving control animals lost the functional operculum and replaced it with a rudimentary one; the other remained unchanged. No reversals occurred in this group.

DISCUSSION

Asymmetry of external structure is not confined to Serpulids. In species of Crustacea in which the adults have asymmetric chelae the juveniles sometimes have two equal-sized claws. They are usually both small, as in the lobster, *Homarus*, and in the fiddler crab, *Uca*. In other genera, such as the Alpheids (snapping shrimp), the two chelae differentiate directly into two distinct types. In the lobster and the alpheids, the alteration of one claw into a different form is a normal

ontogenetic step (Herrick, 1895, 1907; Emmel, 1908; Przibram, 1905, 1931). Morgan (1923, 1924), however, felt that the loss of one of the claws of a juvenile fiddler crab *Uca* fixed the symmetry of the animal. Vernberg and Costlow (1966) on the other hand, did not observe any effect of cheliped removal on laboratory-raised male *Uca* juveniles. In species where the asymmetry is determined by hereditary pattern it is relatively easy to account for the distribution of left- and right-handed members of the population. Even in organisms such as *Alpheus*, the pistol shrimp, in which reversal of chela types can be induced, the population balance is hereditary. Approximately half of the larvae will develop directly into left-handed adults and half, into right-handed ones.

In the Serpulid *Hydroides*, however, the position of the functional operculum does not seem to genetically determined. The great majority of specimens in the adult population of *H. dianthus* sampled were asymmetric with regard to the two opercula, although bioperculate animals appeared in every collection. The first operculum to appear in juvenile animals invariably formed on the left (Zeleny, 1905; 1911; Ichikawa and Takagaki, 1942; Wisely, 1958), but both the population distribution of juvenile groups and the observations made of them demonstrated that they made a rapid transition from an entirely left-handed population at the earliest stages of opercular development to an equilibrium population comprising equal numbers of left-handed and right-handed individuals. Zeleny (1905, 1911) and Wisely (1958) found that one reversal occurred early in juvenile life. This eliminated the primary left operculum and, by growth of the right rudimentary operculum, the animals became right-handed. However, they had no information on how this theoretically right-handed juvenile population became transformed into an asymmetric adult one. In the present study it was found that *Hydroides* juveniles have an ontogenetic pattern which appears to be precisely programmed only through the early post-metamorphic stages. A branchial operculum invariably developed on the left side and the juvenile animal became asymmetric for the first time. The development of this operculum at the apex of Branchia II on the left side was followed either by a loss of pinnules from this branchia or, apparently, by the autotomy of the opercular cup from the tip of the branchial stalk. In the first instance, the branchial operculum was converted directly into a primary functional operculum; but in the latter event, this structure had to be developed *de novo* from the dorsal region of the branchial base. Support for this hypothesis was also provided by the observation that juveniles were frequently found with a small differentiating functional operculum on the left side. The branchial operculum persisted for a variable period of time—several days ordinarily and five weeks in the most extreme case. Zeleny (1911) showed that excision of a portion of the branchial operculum can result in regeneration of the absent part rather than in further developmental changes in opercular structure. In the present work juveniles proceeded to later developmental stages after the amputation of the entire branchial operculum.

Prior to the formation of the primary operculum the juvenile may follow either of the two above pathways, but there were a number of possibilities thereafter. The irregularity of opercular development after the loss of the primary functional operculum implied that environmental circumstances are involved with later opercular events, as is true in adult animals. Ludwig and Ludwig (1954) found that juveniles of *H. norvegicus*, if undisturbed, followed the pattern described by Zeleny (1905, 1911) for specimens of *H. dianthus*. However, if the primary

operculum were amputated, another primary-type operculum would develop on the opposite side. Repeated ablation of these opercula during a period of time equivalent to the normal life-span of the primary operculum (approximately 6 months, according to Zeleny, 1905) resulted in continual reversals involving only primary-type opercula, but at the end of this period a mature functional operculum was formed (Ludwig and Ludwig, 1954). The present work indicates that such repetitive development of a primary-type operculum also occurs frequently under normal conditions in *H. dianthus* juveniles. Rarely was the initial operculum the only primary functional operculum which the juvenile produced during the course of its maturation, as Zeleny (1905, 1911) supposed. In the animals he observed, the primary operculum was supplanted by a mature functional operculum which developed from the rudimentary operculum present on the right side. This pattern cannot explain the appearance of primary-type functional opercula on the right side or even on both sides, as in some bi-operculate juvenile animals. An individual often lost and regenerated a primary type functional operculum one or more times, frequently on the same side. In contrast to Ludwig and Ludwig's (1954) results I found that extirpation of the primary operculum did not lead to its regeneration, but instead, to a static condition with one or two rudimentary opercula, or with no opercula at all. It therefore appeared that in specimens of the Woods Hole region there is no fixed "life-span" for the primary functional operculum. After some time, one of the rudimentary opercula developed into a mature functional operculum and often no more primary type functional opercula were formed in later reversals. There were enough exceptions to the above order of events to indicate the existence of an indeterminate stage in opercular development. During this flexible period the animal might develop, interchangeably, either primary or mature-type opercula. The mechanism for the final maturation or determination of the adult opercular type is unknown. It is not, apparently, rigidly time-determined but it does occur by the time an animal approximates a certain size (2-3 mm) and when the branchiae have become pigmented. By then the capacity of the branchial base tissue to form a single-cupped operculum has been lost.

Most heterochelous crustaceans differ from these polychaetes in that asymmetry is essentially fixed before the attainment of maturity and there is no natural oscillation between asymmetric chelae. The ability to autotomize an operculum or claw under duress and to regenerate it is a useful adaptive mechanism, but the crustacean claw is slowly regenerated. To attain full size it is necessary for several molts to intervene and meanwhile the animal is at a competitive disadvantage. In *Hydroides* adults a missing operculum is readily replaced by the growth of the rudimentary operculum which becomes a functional defensive device within a few days. In juveniles, however, there is little such regularity. In only 12.5% of these animals did the rudimentary operculum enlarge in response to the excision of the primary one. In slightly older animals, such as those with a mature operculum on the right side, 80% reversed under these conditions. These results demonstrate a correlation between the ability of the young animal to reverse and the establishment of a mature functional operculum. Apparently the development both of the mature operculum and of the opercular response system are dependent upon the differentiation and maturation of the juvenile animal. It may be that tissue response is deficient at early ages, or perhaps both processes are dependent upon the maturation of some extra-opercular control system (nervous, hormonal, etc.).

Observations made on specimens of *Hydroides dianthus* of various ages showed that physiological transposition of opercula is a normal pattern in the animals' lives. The result was a series of opercular "oscillations" although no definite periodicity was detected. As soon as a juvenile animal had a rudimentary operculum as well as a functional one, it was theoretically possible for a natural reversal to occur. This did happen, particularly among the older specimens of the juvenile population. Alternatively, at these early stages, the functional operculum (especially if it were a primary-type one) might simply be reproduced on the same side as the autotomized one without any concomitant differentiation of the rudimentary operculum.

There were two patterns by which reversal could be accomplished, in adults or in juveniles. The functional operculum could be cast off first, followed by the differentiation and growth of the rudimentary one. As an alternative mechanism, the rudimentary operculum developed into a functional one even though the old functional operculum was still intact. The older operculum was thereafter autotomized and supplanted by a rudimentary one. The two patterns differ primarily in the timing of the autotomy of the original functional operculum. Bi-operculate animals thus are not aberrant or atavistic specimens, nor do they represent a third stable opercular form. As juveniles became older, right-handed and bi-operculate individuals appeared concomitantly. By the time the animals were 2 to 3 mm long they had established a 1:1 left-right opercular ratio, but there were elevated proportions of bi-operculate specimens. Paired functional opercula occur when by some means the rudimentary operculum overcomes the "inhibition" of the functional operculum and becomes capable of enlargement and development. The two opercula are unable to co-exist for long in this balanced state, and one of them, generally the older, is autotomized and replaced by a rudimentary operculum. Therefore bi-operculate animals can be regarded as indicators of reversal. The elevated frequency of bi-operculate animals in the young sample paralleled the enhanced reversal rate found in this group whereas the adult samples showed both fewer bi-operculate members and a lower reversal rate.

There was a slight tendency in young animals to autotomize the functional operculum and to replace it with a new functional operculum on the same side, although this was much less marked than in juvenile specimens. In older animals loss of an operculum was almost always followed by reversal. However, as the worm aged, the tendency to reversal became increasingly retarded, which might be a concomitant of a general metabolic slowdown. The rudimentary operculum enlarged more slowly, and if the animal became bi-operculate both opercula could be maintained for several weeks. A similar phenomenon was found in such species as *Alpheus*, in which the rate of claw inversion and the ability to reverse are inversely proportional to the size (*i.e.*, age) of the animal (Przibram, 1908, 1931; Huxley, 1932). In older animals transposition was virtually precluded (Huxley, 1932). This is related to alterations in the growth rates of the heterogonic chelae; the relative rates of growth have changed so that reversal can no longer be induced (Dawes, 1934; Huxley, 1932). In *Hydroides*, in contrast, natural inversion continues throughout life, albeit at a decreasing frequency. In *Hydroides* juveniles the functional operculum is enormously exaggerated with respect to the tiny body, so the operculum must, like the cheliped, slow its initial growth rate. As the animal elongates the operculum becomes increasingly shorter in proportion to body length. Whether negative allometry is intimately related to the phenomena

controlling reversal or whether they are merely congruent phenomena has not been determined.

How can opercular reversal be accounted for? Opercular aging is one postulate to explain the physiological reversals found in specimens of *Hydroides*. Ichikawa and Takagaki (1942) proposed that there might be an aging of the functional operculum since they found that in bi-operculate individuals one of the opercula always appeared older and less active than the other. Wrinkled, necrotic opercula were occasionally observed in both normal and bi-operculate adult individuals in the present population as well. W. Ludwig (1941) and Ludwig and Ludwig (1954) claimed they could distinguish aging opercula by vital staining and thus predict reversal events. Aging, they postulated, was correlated with the decline in production of some specific chemical agent which inhibits the rudimentary operculum and maintains the vitality of the functional one.

Opercula of dissimilar ages may respond differently to experimental manipulation, also suggesting a natural cycle for the operculum. Abeloos (1952b) noted that amputation of an old functional operculum resulted in a conventional reversal, but that when the same operation was performed on a newly-developed one, it was replaced by another functional one on the same side. This phenomenon has also been noted in young animals and juveniles (see above) and it may be characteristic of organisms and structures in a still-differentiating state. Ludwig and Ludwig (1954) removed the upper cup of one functional operculum in bi-operculate animals and found that if the functional operculum were the older structure it was autotomized; if younger, it remained until it became senescent. If both cups were removed the older of the two opercula was autotomized and replaced by a new one, whereupon the second of the two opercula dropped off.

Arguing against a regular aging process as a determinant of natural reversal are the comparisons of reversal rates in the various groups kept in the laboratory. These indicated that opercular changes were random, in that animals which had recently reversed did not subsequently show enhanced or depressed rates of reversal. Each event was apparently independent. The substantially enhanced rates of change in field-maintained animals demonstrated that many alterations can be accredited to predation and other environmental factors. The major predators of *Hydroides* are probably sea urchins, crabs and other small Crustacea, and various molluscs. Branchial and opercular cup losses noted in the field group were obviously traumatic events and not degenerative ones, as the animals rapidly regenerated new branchiae and opercula. Alterations in most of this population were therefore not attributable to abnormalities, although there might have been greater physiological activity in the sea than in sub-optimal laboratory conditions. In addition, laboratory animals could have been hindered by removal from the tube.

Once a left-right equilibrium of opercula had been established in the *Hydroides* population, it was maintained in a dynamic state by a combination of physiologically-controlled oscillation and environmental stress. Both seemed requisite to account for the differences in reversal rate between the laboratory population and those animals kept in a natural situation. In the field experiments, the loss of opercula to predators was superimposed on the intrinsic reversal pattern of the individuals in the population to create a high rate of flux. At present it is difficult to determine the intrinsic factors which promote reversal, and discussion of chemical agents is purely speculative.

I wish to thank my advisor, Professor Richard J. Goss, for his valuable guidance during the course of this project, and in addition to acknowledge the advice of Dr. Louis Homer on the statistical handling of the data.

SUMMARY

Although any population of *Hydroides dianthus* maintains an equilibrium of equal proportions of right- and left-handed animals, individual members are continually modifying their condition. They may spontaneously autotomize the functional operculum, permitting the rudimentary one to enlarge. Alternatively, the rudimentary operculum may develop independently to yield an unstable situation in which the animal bears two large opercula. This may persist for several weeks; then the older of the two opercula autotomizes. Either mechanism results in a reversal of the original opercular asymmetry. The rate of variation in left- and right-handed individuals is equal, so that population balance does not shift even though its component organisms undergo continual flux.

Each animal undergoes several reversals during a normal life span, beginning with the larval stages. The rate of change declines gradually so that the older the animals, the less frequently it will reverse. Animals maintained in the ocean subject to predators show a high rate of reversal and traumatic aberrations.

In larval ontogeny the origin of an opercular cup on the second left branchial rudiment is followed by (a) loss of pinnules on the opercular stalk to form the primary operculum or (b) severance of the opercular cup from the branchia, perhaps by progressive attenuation of the terminal end of the filament. In the latter case, a primary operculum must be developed on the left. This seems to be accomplished by the formation of a left rudimentary operculum, developing later into a primary one. This operculum, no matter how it originates, may either be lost and replaced by a similar structure, or reversal may occur. These processes may be repeated until this simple operculum is permanently replaced by an adult double-cupped operculum. The time at which this occurs is not fixed, and there is a transitional period during which either type of operculum can appear. After further maturation, only the adult type of functional operculum can be formed. This coincides with the development of the ability to carry out opercular regulation.

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